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SUPPLEMENTARY DESCRIPTION AND PHYLOGENETIC SIGNIFICANCE OF *ARCOSCALPELLUM CONRADI* (GABB) (CIRRIPEDIA: SCALPELLIDAE) FROM THE PALEOCENE VINCENTOWN FORMATION OF NEW JERSEY

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Abstract.—The capitulum and peduncular armament of *Arcoscalpellum conradi* (Gabb) are described on new material from the upper Paleocene (Thanetian) Vincentown Formation in New Jersey. This species, together with the lower Paleocene (Danian) species *A. toulmini* Weisbord from Alabama and *A. elongatum* (Steenstrup) from Denmark, are derivatives of the Upper Cretaceous *A. fossula* (Darwin) group, and are representative of the ancestral stock that gave rise to eastern North American Eocene species of *Arcoscalpellum* Hoek.

The events leading to the mass extinction of invertebrate and vertebrate groups near the end of the Cretaceous (Maastrichtian Stage) also affected the cirriped fauna. As illustrated in Fig. 1, the late Cretaceous fauna was diverse and, considering the large number of holdover species, developed under relatively stable environmental conditions. Conditions responsible for the demise of the Cretaceous fauna appear to have originated with the onset of the Maastrichtian. Whereas the percentage of holdover species in Cenomanian through Campanian faunas averaged over 60%, the percentage of holdover species in the Maastrichtian dropped to 28%. After significant species diversification during the Maastrichtian, 95% of the fauna became extinct by the close of the Cretaceous, with only two species, *Zeugmatolepas cretae* (Steenstrup) and *Verruca prisca* Bosquet surviving into the early Paleocene (Danian Stage). Several genera also became extinct by the end of the Maastrichtian, including the lepadomorphs *Cretiscalpellum* Withers, *Loriculina* Dames, *Stramentum* Logan, *Titanolepas* Withers and *Virgiscalpellum* Withers, the brachylepadomorph *Brachylepas* Woodward, and the verrucomorph *Proverruca* Withers.

Only fifteen cirriped species, including seven lepadomorphs, three verrucomorphs, two brachylepadomorphs, and three balanomorphs, have been reported from Paleocene rocks (Table 1). The surviving Paleocene fauna, as currently understood, was exceedingly depauperate. How much of this record is related to a lack of Paleocene localities preserving suitable environments is unknown. Certainly Paleocene exposures are more restricted in areal extent than those of the Upper Cretaceous, but even shallow marine Paleocene deposits with well-preserved shelly invertebrates exhibit very low diversity in the cirriped component of their faunas.

The Paleocene fauna, and particularly that of the Danian, is clearly transitional between those of the Cretaceous and the Eocene (Fig. 2). With the exception of the Australasian records of *Bathylasma* Newman and Ross, *Pachylasma* Darwin, and *Eolasma* Buckeridge, all of the recorded Paleocene genera are represented in the Cretaceous, and only one genus, *Zeugmatolepas* Withers, became extinct prior to the Eocene. It is, thus, from the Paleocene survivors of the Cretaceous that the modern cirriped fauna was derived.

This study, based on new material from the Paleocene of eastern North America,

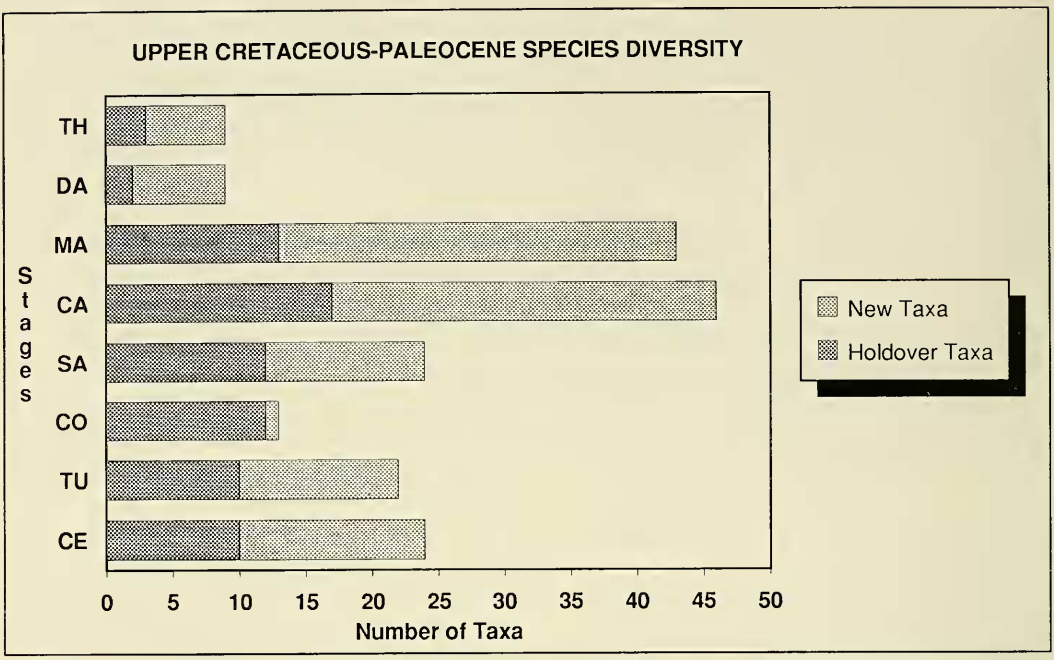

Fig. 1. Cirriped species diversity during the Late Cretaceous and Paleocene. Stage name abbreviations are, from oldest to youngest: CE, Cenomanian; TU, Turonian; CO, Coniacian; SA, Santonian; CA, Campanian; MA, Maastrichtian; DA, Danian; TH, Thanetian.

evaluates the relationship of the four known Paleocene species of *Arcoscalpellum* Hoek to the more diversified faunas of the Upper Cretaceous and Eocene (Fig. 3). Foster (1980) proposed the genus *Graviscalpellum* for species previously included in *Arcoscalpellum* that are hermaphroditic and whose lower latera are no more than one-tenth the height of the capitulum. As modified by Buckeridge (1983), Australasian fossil species of *Graviscalpellum* can be recognized by the lack of pits for complemental males on the inner surface of the scutum above the adductor muscle scar, the very low and broad rostral latus, the diminutive size of the other lower latera, and the apical umbones of the capitular plates. In all these regards, North American Paleocene and Eocene species of *Arcoscalpellum* are readily included in the genus *Graviscalpellum.* However, as noted by Foster (1980), the extant species attributed to *Graviscalpellum* range over five of the genera of extant Arcoscalpellinae described by Zevina (1978). Until the classification and nomenclature of extant arcoscalpellines can be unravelled, the North American Paleogene species will be referred to the genus *Arcoscalpellum* in the broader sense of Withers (1953).

The two species of *Arcoscalpellum* Hoek from North America are *A. toulmini* Weisbord from the Danian Porters Creek Formation in Alabama (Weisbord, 1977), and *A. conradi* (Gabb) from the Thanetian Vincentown Formation in New Jersey. Both were described from scanty material. *Arcoscalpellum toulmini* was described from two scuta and two terga, and *A. conradi* from the type lot of two fragmentary carinae and a scutum, and a questionable tergum illustrated by Weller (1907). Collections made by R. T. Perreault from the lower unnamed member and the Matthews Landing Member of the Porters Creek Formation in Wilcox County, Alabama include carinae, terga, scuta, upper latera, carinal latera, rostral

Table 1.—The Paleocene record of the cirriped order Thoracica.

Age	Taxon	Locality	Authority
Danian	*Zeugmatolepas cretae* (Steenstrup)	Denmark	Withers (1935)
	Scillaelepas dorsata (Steenstrup)	Denmark	Withers (1935)
	Arcoscalpellum elongatum (Steenstrup)	Denmark	Withers (1935)
	A. danicum (Brünnich Nielsen)	Denmark	Withers (1935)
	A. toulmini Weisbord	Alabama	Weisbord (1980)
	Verruca prisca Bosquet	Denmark	Withers (1935)
	V. rocana Steinman	Argentina	Withers (1935)
	Pycnolepas bruennichi Withers	Denmark	Withers (1935)
Thanetian	*Smilium calanticoideum* Buckeridge	New Zealand; Chatham Islands	Buckeridge (1983)
	Arcoscalpellum conradi (Gabb)	New Jersey	This paper
	Verruca rocana Steinman	North Carolina	Zullo & Baum (1979)
	Verruca tasmanica chatheca Buckeridge	Chatham Islands	Buckeridge (1983)
	Pycnolepas landenica Withers	Belgium	Withers (1953)
	Eolasma maxwelli Buckeridge	New Zealand; Chatham Islands	Buckeridge (1983)
Paleocene (undifferentiated)	*Pachylasma veteranum* Buckeridge	Chatham Islands	Buckeridge (1983)
	Bathylasma rangatira Buckeridge	Chatham Islands	Buckeridge (1983)

latera and peduncle plates. These plates are smaller than the types of *A. toulmini* and probably represent juveniles. Exhaustive sampling by H. Mendryk of three localities in the Vincentown Formation has yielded numerous well-preserved scuta, terga, carinae, upper latera, lower latera, and peduncle plates of *A. conradi*. The only plate missing for both of these species is the rostrum. The following discussion is based on a redescription of the capitular armature of *A. conradi*. The description of the Danian Porters Creek fauna, including a supplementary description of *A. toulmini*, is the subject of a forthcoming paper.

Family Scalpellidae Pilsbry, 1916
Subfamily Arcoscalpellinae Zevina, 1978
Genus *Arcoscalpellum* Hoek, 1907
(broad sense)
Arcoscalpellum conradi (Gabb, 1876)
Figs. 4, 5

Scalpellum conradi Gabb, 1876:179, pl. 5, figs. 3–4.—Johnson, 1905:28.—Weller, 1907:845, pl. 110, fig. 10.—Russell, 1967: 1546.—Richards, 1968:218.

Scalpellum (*Arcoscalpellum*) *conradi* Gabb: Withers, 1935:276, pl. 34, figs. 10a–b, 11a–b.

Arcoscalpellum conradi (Gabb): Weisbord, 1980:132, pl. 12, figs. 16–19.

Lectotype.—Basal part of carina, Academy of Natural Sciences of Philadelphia no. 4655 (designated by Withers, 1935).

Lectotype locality.—Vincentown Formation, Vincentown, Burlington County, New Jersey.

Emended diagnosis.—Intraparietes of carina very narrow, inset from parietes, extending from apex to near basal margin; tergal and lateral margins of scutum nearly equal in length; carinal segment of tergum narrow, usually less than one-fourth width of plate; occludent margin of tergum straight, about one-half length of scutal margin; umbo of upper latus apical; carinal latus triangular, broader than high, with incurved apex, apical umbo, and striated carinal segment.

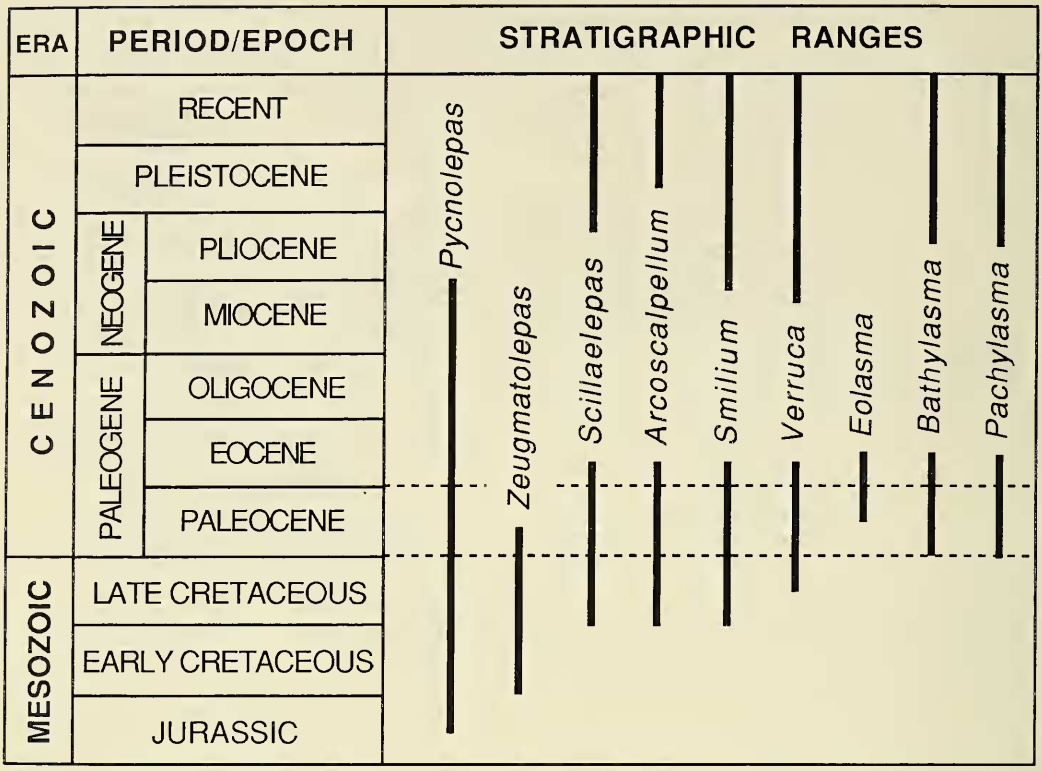

Fig. 2. Stratigraphic distribution of cirriped genera known from Paleocene strata.

Supplementary description.—Carina thin and markedly convex in side view; height averaging five and one-half times greatest width; apex narrow, acute; tectum nearly flat in apical region, but becoming gently arched in lower two-thirds, and broadening markedly toward basal margin; tectum ornamented by low, V-shaped growth increments, an indistinct median longitudinal ridge, and faint, irregularly-spaced, longitudinal striae, and bordered on both sides by narrow ridges; bordering ridges prominent in apical region, but fading toward basal margin; parietes narrow, markedly concave, offset from parietes at an angle of about 80°; intraparietes broad and thin in apical region, becoming very narrow and broadly rounded in basal region; intraparietes inset from parietes and at right angle to tectum; basal margin very thin, broadly V-shaped to gently rounded.

Scutum trapezoidal, height averaging twice width, strongly convex in cross section; gently arcuate apicobasal ridge dividing plate into subequal halves, with tergal side narrower than occludent side; apicobasal ridge distinct, broadly rounded in juvenile scuta, becoming indistinct and narrow in adults; exterior ornamented by moderately broad growth increments bearing fine, closely-spaced growth ridges, and often with a few, faint, irregularly-spaced ridges extending from apex to basal margin on either side of apicobasal ridge; apex acute, slightly curved toward tergum; tergal margin slightly concave, about equal in length to straight lateral margin; tergolateral angle obtuse, sharp to broadly rounded; basitergal angle sharp, about 90°; basal margin slightly convex; rostral angle acute, projecting slightly downward, about 90°; occludent margin convex and parallel to lateral mar-

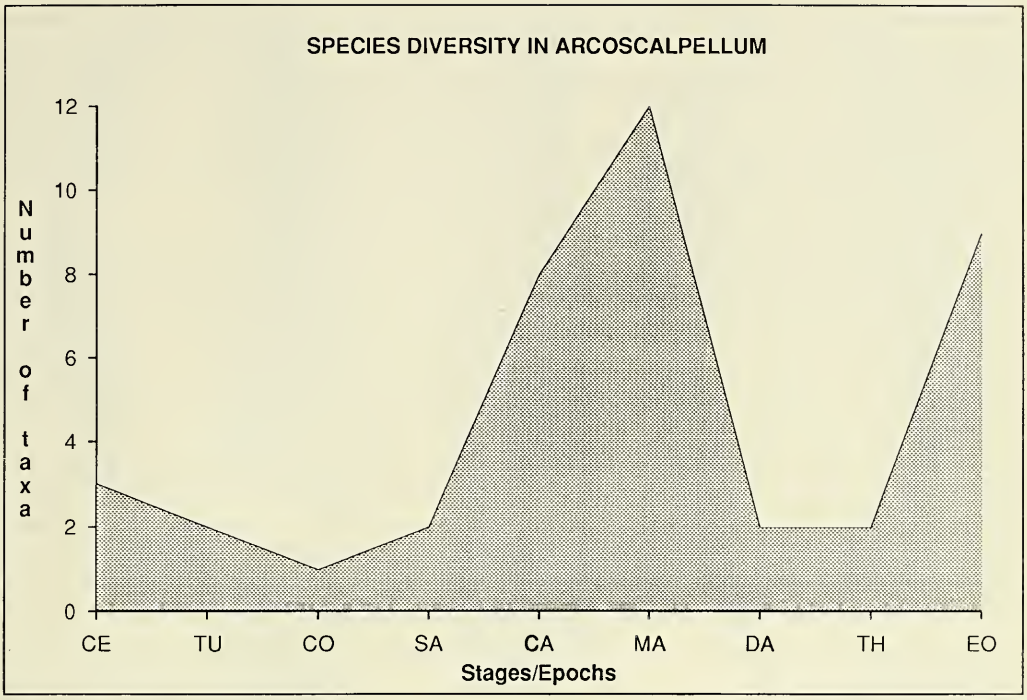

Fig. 3. Number of species ascribed to the genus *Arcoscalpellum* during the Late Cretaceous, Paleocene and Eocene (EO). Cretaceous and Paleocene stage name abbreviations as in Fig. 1.

gin; adductor muscle scar large, ovate, shallow, placed on the occludent side of the center of the plate; flattened inner surface of occludent margin narrow; thin ridge delimiting narrow, shallow, internal groove along upper part of occludent margin extends from near apex to midpoint of occludent margin; another indistinct, broadly rounded ridge roughly paralleling tergal margin extends from near apex to intersect lateral margin at point two-thirds the distance from basitergal angle to tergolateral angle; interior of apex and uppermost part of tergal margin marked by fine growth ridges.

Tergum flat, triangular, narrow, length from two to two and one-half times width, with narrow, low, nearly straight apicobasal ridge; exterior ornamented by broad growth increments bearing fine, closely-spaced growth ridges; central third of plate exterior on scutal side of apicobasal ridge often marked by narrow, regularly-spaced radial striae; apex acute, not arched toward carinal side; carinal segment of plate narrow, usually less than one-fourth width of plate, rarely up to one-third width of plate, not well-differentiated into upper and lower halves; carinal margin broadly convex; scutal margin very slightly convex, often marked at midpoint by slight angulation and change in direction of growth ridges; scutal margin nearly twice length of straight occludent margin; basal angle narrowly V-shaped; interior of tergum smooth, except for reflection of growth increments, narrow groove marking position of apicobasal ridge, and a few, short, thin, vertical ridges immediately below apical shelf; apical shelf narrow, delimited from interior of tergum by prominent narrow ridge extending from apex along occludent and upper carinal margins, and marked by fine growth ridges.

Upper latus flat, except for narrow, shallow sulcation along scutal margin, higher

than wide, hexagonal in juvenile specimens, becoming quadrangular in adults, and slightly bowed toward scutum; umbo apical; exterior ornamented by growth ridges crossed by irregularly-spaced, indistinct radial striae; scutal and tergal margins straight; scutal margin bordered by prominent narrow ridge; tergal margin about eight-tenths length of scutal margin; basal margin of juvenile specimens divided into three or four unequal segments bounded by low, narrow apicobasal ridges; scutal segment of basal margin narrow, straight, upturned, about four-tenths length of broadly convex to angulate central segment; carinal segment slightly shorter than central segment, nearly straight, markedly upturned, and parallel to scutal margin; marked angulation between scutal and central segments of basal margin lost in adults; interior flat, smooth, except for beveled carina and scutal margins in adult specimens.

Carinal latus triangular, one and one-half times wider than high, with incurved apex and apical umbo; exterior ornamented by prominent growth ridges crossed by regularly-spaced radial striae on carinal side; broad, low, slightly arcuate, apicobasal ridge bordering striate surface of plate intersects basal margin to the scutal side of midpoint of basal margin; upper margin concave, marked by narrow ridge bearing upturned growth lines, and bearing thin, broad shelf inflected about 90° to plate; carinal margin gently convex; basal margin slightly concave, except slightly convex near intersection with upper margin.

Inframedian latus triangular, leaning toward scutum, low and broad, with width averaging twice height; rostral margin concave, slightly more than one-half length of nearly straight carinal margin; basal margin gently concave; umbo apical or slightly removed from apex; apex produced, forming acute point; exterior ornamented by closely-spaced, flat growth increments.

Rostral latus arcuate, very low and broad, with width about five times height; prominent, narrow, upwardly convex ridge extends from umbo across plate to lower part of rounded inframedian lateral margin; upper margin strongly convex; basal margin strongly concave; rostral margin truncate; inner surface divided into two equal halves by sharp, narrow ridges extending the breadth of the plate.

Rostrum unknown. Peduncular plates low and broad, with convex upper margin shorter than concave to straight lower margin.

Discussion.—The carinae and upper latera from the Vincentown Formation first appeared to represent two distinct species of *Arcoscalpellum,* but on further examination were recognized as growth stages of the same species. The juvenile carina has broad, very thin intraparietes developed for a short distance below the apex. In some instances, the upward growth of the intraparietes slightly offset the umbo from the apex plate. The juvenile tectum is relatively flat and bordered by prominent ribs. With growth, the tectum widens considerably, the bordering ribs become narrow and rather indistinct, and the intraparietes narrow and thicken appreciably. The broad, delicate intraparietes of the apical region are missing in adult carinae, being lost through abrasion during the life of the individual, or as a result of the fossilization process. The juvenile upper latus is sharply pentagonal to hexagonal as the result of the tripartite to quadripartite division of the basal margin. As is shown by the progression of growth increments, adult upper latera gradually lose the angulation between the scutal and central segments of the basal margin and become quadrilateral.

Arcoscalpellum conradi differs primarily from *A. toulmini* in plate proportions. The tergum of *A. conradi* is narrower, and has a much narrower carinal segment, but in other respects is very similar to that of *A. toulmini.* The scuta of the two species are also quite similar, differing primarily in the length of the tergal margin, which is considerably longer in *A. conradi.* New collections of *A. toulmini* plates made by R. T. Perreault from the Porters Creek Formation

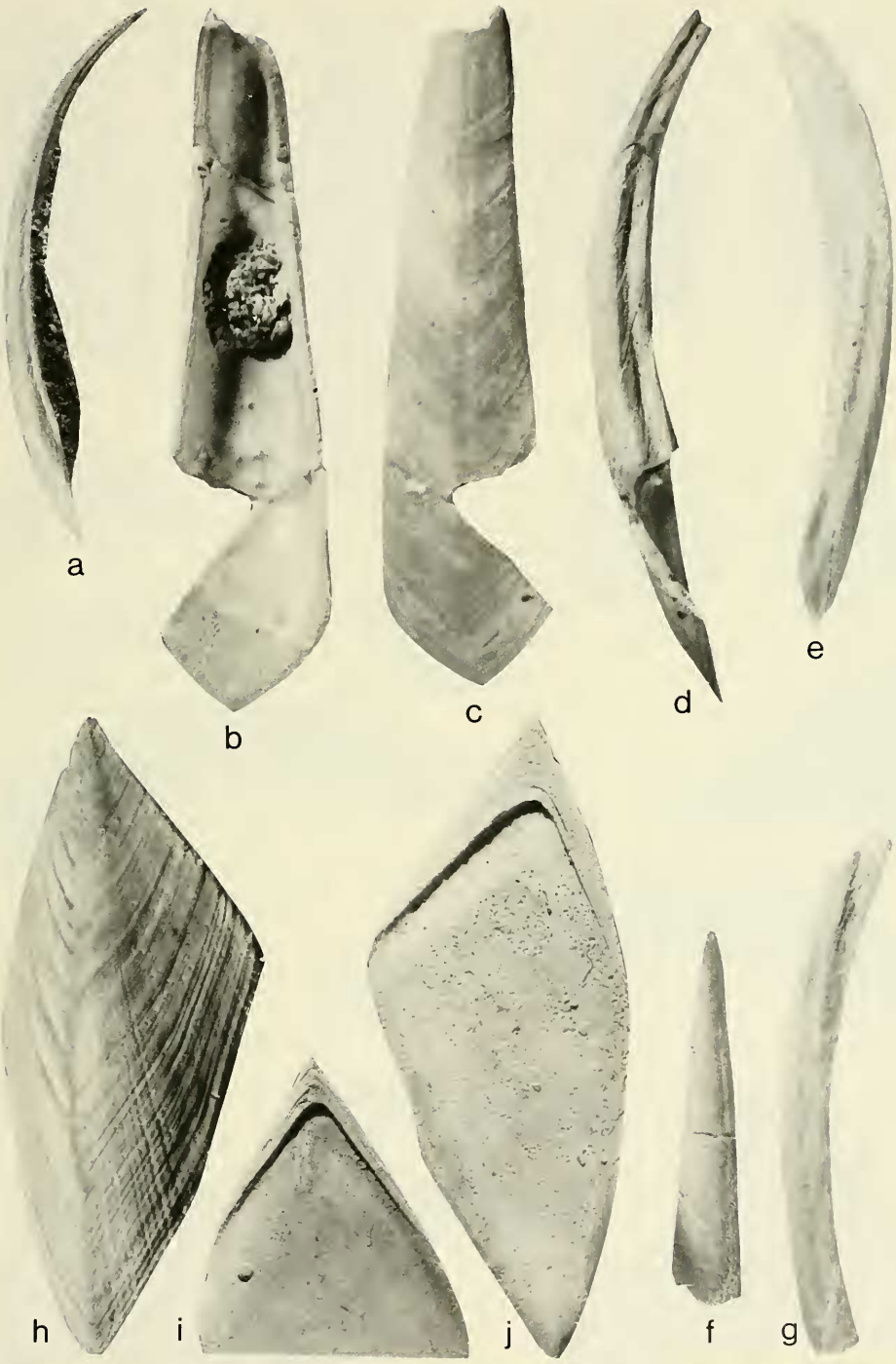

Fig. 4. Carinae and terga of *Arcoscalpellum conradi* (Gabb): a, side view of carina, hypotype USNM 444307; b–d, inner tectal and side views of carina, hypotype USNM 444308; e, side view of juvenile carina, hypotype USNM 444309; f, tectal view of juvenile carina, hypotype USNM 444310; g, side view of juvenile carina with umbo removed from apex, hypotype USNM 444311; h and j, exterior and interior view of tergum, hypotype USNM 444312; i, interior of apex of tergum showing vertical ridging, hypotype USNM 444313; a–d, h–j, ×4; e–g, ×10.

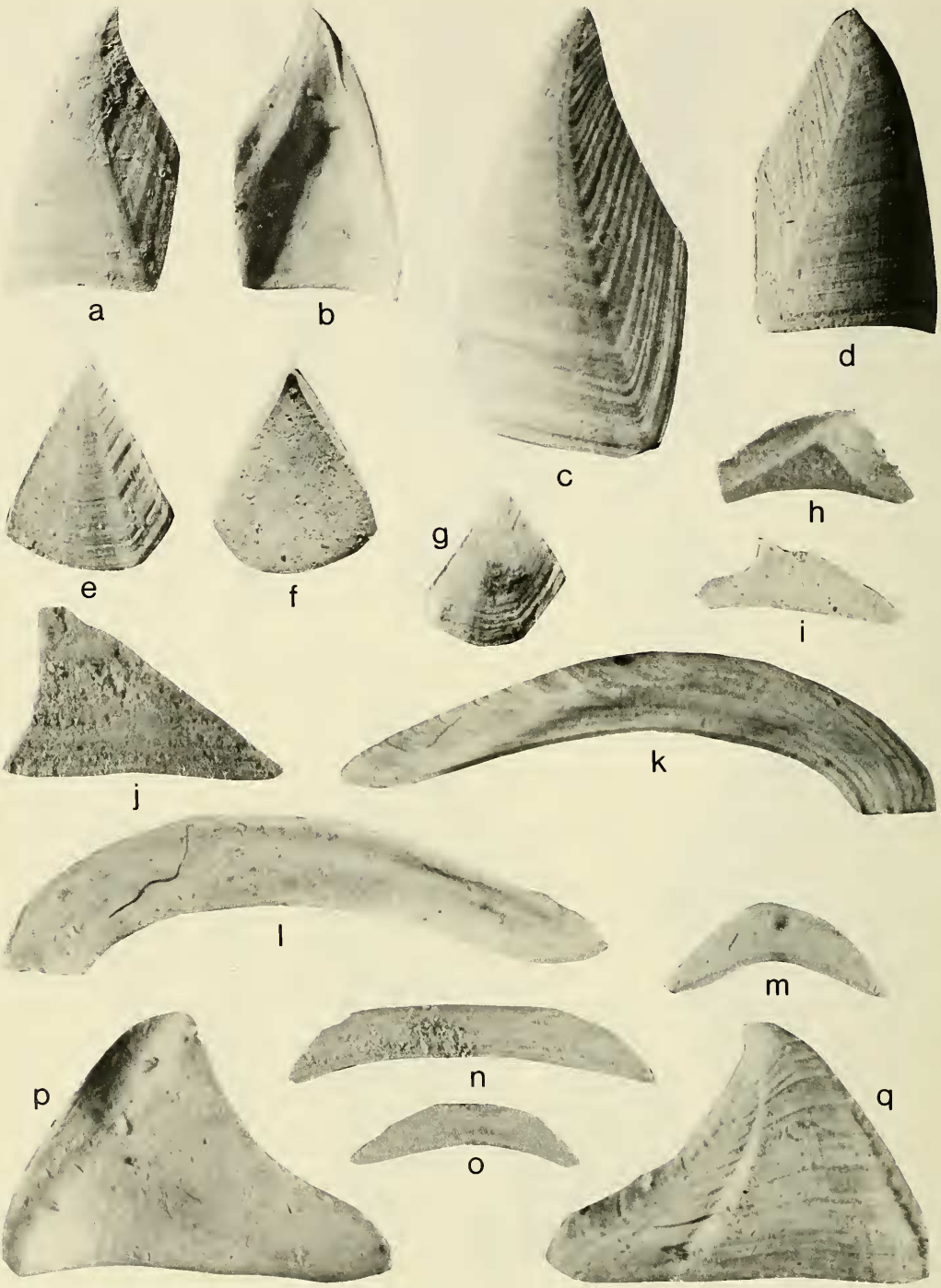

Fig. 5. Scuta, upper and lower latera, and peduncle plates of *Arcoscalpellum conradi* (Gabb): a–b, interior and exterior of scutum with well-developed apicobasal ridge, hypotype USNM 444314; c, exterior of scutum with moderately-developed apicobasal ridge, hypotype USNM 444315; d, exterior of scutum with typical apicobasal ridge, hypotype USNM 444316; e–f, exterior and interior of quadrilateral upper latus, hypotype USNM

in Alabama include carinae, terga, scuta, upper latera, carinal latera, rostral latera and peduncle plates. These plates are smaller than the types of *A. toulmini* and probably represent juveniles. The carina is similar to that of juvenile *A. conradi,* but lacks both a median and bordering longitudinal ridges. The carinal latus is similar, but is higher than wide and the basilateral angle is not produced. The rostral latus lacks the prominent external ridge diagonally traversing the breadth of the plate.

The Danish Danian species *A. danicum* is known only from a broken tergum, which resembles that of *A. conradi* in the narrowness of its carinal segment, but differs in the much greater overall width of the plate, the apparently longer scutal margin, and the markedly more arcuate apicobasal ridge. The scutum of the other Danian species from Denmark, *A. elongatum,* is remarkably similar to that of *A. conradi,* but the other plates differ substantially. The tergum of *A. elongatum* and its carinal segment are much broader, and the angle between the upper and lower carinal margins is better delimited. The upper latus is much narrower, the carinal latus lacks longitudinal striation on the carinal side, and the tectum of the carina is subcarinate.

Occurrence.—Upper Paleocene (Thanetian), Vincentown Formation, New Jersey. Previous records: lectotype locality, basal half of carina (lectotype), scutum (Gabb, 1876); Timber Creek, apical half of carina (Gabb, 1876); Hurfville, Gloucester County, ?tergum (Weller, 1907). New records: locality 1, over 200 carinae, over 300 scuta, over 300 terga, over 100 upper latera, over 100 carinal latera, 11 inframedian latera, 33 rostral latera, and over 100 peduncle plates; locality 2, nine partial carinae, six partial scuta, four partial terga, two upper latera, eight carinal latera, two partial rostral latera, nine peduncle plates; locality 3, five partial carinae, three scuta, three terga, one upper latus, one carinal latus.

Repository.—Hypotypes USNM 444307 through 444326, and hypotype lots USNM 444327 through 444329 are in the Department of Paleobiology, National Museum of Natural History, Washington, D.C.

Phylogenetic Considerations

Withers (1935) described three informal groups for the majority of Cretaceous species of *Arcoscalpellum*: the group of *A. arcuatum* (Darwin); the group of *A. fossula* (Darwin); and the group of *A. maximum* (J. de C. Sowerby). Although Withers did not provide diagnoses for these groups, they are readily distinguished by their carinae. The tectum in the *A. arcuatum* group is arched, broadens rapidly toward the base, has a median longitudinal ridge and prominent bordering ridges, and intraparietes that are bent inward at nearly right angles to the parietes. The carina in the *A. maximum* group is distinguished by its narrow apex and broad base, wide intraparietes at nearly right angles to the tectum, and longitudinal ridges separating the narrow parietes from the intraparietes. The tectum in the *A. maximum* group is arched, and bears median longitudinal and bordering ridges, but these are less prominent than the tectal ridges in the *A. arcuatum* group. The median ridge on the tectum in the *A. fossula* group is either greatly reduced or absent, the tectum is flat, and the plate is narrow throughout its length. Although prominent, the intraparietes are

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444317; g, exterior of juvenile hexagonal upper latus, hypotype USNM 444318; h, interior of inframedian latus, hypotype USNM 444319; i, interior of inframedian latus, hypotype USNM 444320; j, exterior of inframedian latus, hypotype USNM 444321; k–l, exterior and interior of rostral latus, hypotype USNM 444322; m–o, exterior of peduncle plates, hypotypes USNM 444323, 444324 and 444325, respectively; p–q, interior and exterior of carinal latus, hypotype USNM 444326; a–f, ×4; h–q, ×10.

considerably less developed than those in the *A. maximum* group. Older Cretaceous species of the *A. fossula* group bear prominent ridges separating the tectum from the parietes, but in the Maastrichtian species *A. gracile* (Bosquet) these ridges are greatly reduced.

Representatives of the *A. maximum* and *A. fossula* groups are present in the Upper Cretaceous of eastern North America (Collins 1973, Zullo 1987). The *A. maximum* group is represented by *A. hubrichti* Collins from the lower Campanian of Mississippi and Alabama and *A. bakeri* Collins from the lower Maastrichtian of Mississippi and Delaware. *Arcoscalpellum campus* Collins from the Maastrichtian of Mississippi and *A. withersi* Collins from the Maastrichtian of Mississippi, Alabama, and Delaware represent the *A. fossula* group.

Based on carinal morphology, the Paleocene species of *Arcoscalpellum* appear to have been derived from the *A. fossula* group. All have flat or gently arched tecta, the median ridge is either lacking or subdued, and the bordering ridges are reduced in prominence. The carina is relatively narrow throughout its length, and the intraparietes are greatly reduced in width. As noted previously by Withers (1935) for *A. conradi,* the general form of the capitular plates of the North American Paleocene species compares favorably with that of *A. fossula* and *A. gracile,* differing primarily from the former in lacking prominent external radial ornament. The *A. fossula* facies is continued in the eastern North American Eocene species, *A. subquadratum* (Meyer and Aldrich) from the Calibornian and *A. jacksonense* Withers from the Jacksonian, with additional reduction in: 1) overall carinal width; 2) prominence of the ridges bordering the tectum; and 3) width of the parietes and intraparietes.

Vincentown Formation Locality Descriptions

1. Outer side of large meander on South Branch of Rancocas Creek, 0.75 km north of intersection of Church and Red Lion Roads at Vincentown, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.
2. Outer side of meander on South Branch of Rancocas Creek, 0.5 km southwest of gaging station and 1.25 km north-northwest of intersection of Church and Red Lion Roads at Vincentown, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.
3. Tributary to South Branch of Rancocas Creek, approximately 1.5 km south-southwest of Golden Pheasant Country Club, Mt. Holly 7.5′ quadrangle, Burlington County, New Jersey.

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